



The wing venation of Odonata

John W. H. Trueman* and Richard J. Rowe

Research School of Biology, Australian National University, Canberra, Australia

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Existing nomenclatures for the venation of the odonate wing are inconsistent and inaccurate. We offer a new scheme, based on the evolution and ontogeny of the insect wing and on the physical structure of wing veins, in which the veins of dragonflies and damselflies are fully reconciled with those of the other winged orders. Our starting point is the body of evidence that the insect pleuron and sternum are foreshortened leg segments and that wings evolved from leg appendages. We find that all expected longitudinal veins are present. The costa is a short vein, extending only to the nodus, and the entire costal field is sclerotised. The so-called double radial stem of Odonatoidea is a triple vein comprising the radial stem, the medial stem and the anterior cubitus, the radial and medial fields from the base of the wing to the arculus having closed when the basal sclerites fused to form a single axillary plate. In the distal part of the wing the medial and cubital fields are secondarily expanded. In Anisoptera the remnant anal field also is expanded. The dense crossvenation of Odonata, interpreted by some as an archdictyon, is secondary venation to support these expanded fields. The evolution of the odonate wing from the palaeopteran ancestor – first to the odonatoid condition, from there to the zygopteran wing in which a paddle-shaped blade is worked by two strong levers, and from there through grade Anisozygoptera to the anisopteran condition – can be simply explained.

Keywords: wing origin and structure; venational homologies; wing vein naming systems; dragonfly

Introduction

The wing venation of Odonata has long been regarded as difficult, as is evidenced (see next section) by the fact that numerous nomenclatures have been proposed but all have their critics. Communication is hampered when different authors use different names for the same vein or apply the same name to different veins, and disagreement indicates that the homologies to other orders are unclear. This journal recommends (IJO, 2018) the system of Riek and Kukalová-Peck (1984), hereafter R&KP, but, as will be shown, that nomenclature makes extraordinary demands on the evolution of the veins, is not compatible with the phylogeny, and is one of the most unnatural systems so far proposed. Unfortunately, the available alternative nomenclatures all have obvious flaws. We propose to begin again.

We start with an overview of the wing vein naming system for winged orders other than Odonata, together with a brief survey of the major proposals for Odonata to indicate the extent of past disagreements. We next summarise the current scientific understanding of how insect wings evolved, how they develop and how the veins are formed. These works establish physical and developmental constraints on the evolution of the venation. We then re-examine the odonate

*Corresponding author. Email: truemanic@gmail.com

wing using simple light microscope observation backed by a little scanning electron microscopy. We find that odonates have the same wing veins as all other winged insects, in the same sequence, on the same wing surfaces, and with the same pattern of stemmed and unstemmed veins. The differences are only a matter of relative proportion, some fields having become narrowed or sclerotised while others are expanded.

Like us, R&KP claim to have found in Odonata all the same veins as in other insects, but their system invokes vein mergers, “lost crossings” and the relocation of veins from one wing surface to the other, all of which in evolutionary terms are highly implausible. Our scheme, in contrast, makes no impossible demands on vein evolution and accords with all lines of morphological, genetic, developmental, and phylogenetic evidence. The inter-ordinal and intra-ordinal homologies are straightforward.

Wing vein naming systems

Any reputable textbook on entomology (e.g. CSIRO, 1970, 1991; Grimaldi & Engel, 2005; Gullan & Cranston, 2014; Tillyard, 1926; Triplehorn & Johnson, 2005) will include a diagram of the wing venation of a generalised neopteran insect. The arrangement of the veins is not disputed. The nomenclature in common use is derived from that of Comstock and Needham (1898–1899) who standardised the names of six pairs of longitudinal veins which extend from sclerites at the base of the wing. A seventh pair occurs in a posterior position in some orders. A short eighth pair, located at the anterior basal corner, was described by Kukalová-Peck (1983) in some early fossils and is often (e.g. in Gullan & Cranston, 2014, figure 2.23) but not always (e.g. in Grimaldi & Engel, 2005, figure 4.5) included in the diagram. Each vein pair shows, in one or more neopteran or palaeopteran orders, an anterior branch on the upper wing surface followed by a posterior branch on the lower wing surface. The pairs are named the precosta, costa, subcosta, radius, medius, cubitus, anal and jugal veins. The usual short-form labels are PC, C, Sc, R, M, Cu, A and J. Branches may be conveniently indicated by suffixes A or P and their development on the upper or lower surface by + or –. Veins may branch directly from the basal sclerite or from a stem.

The Ephemeroptera fit into this nomenclature without any difficulty. The ordinal-level peculiarities include partial desclerotisation of the basal portions of veins behind the radius and narrowing at the wing base, together with some fusion of the sclerites to which the muscles attach. Morphologists from Snodgrass (1935) onwards agree that the wing veins of Mayflies map to those of Neoptera, and the sclerites and thoracic muscles themselves are homologous (Büsse, Genet, & Hörnschemeyer, 2013; Willkommen, 2008).

The problem has long been to fit Odonata into this scheme. There are fewer apparent main longitudinal veins than in the other orders, but many more crossveins; together with several features, including a nodus and arculus in all suborders and a triangle in Anisoptera, that are not found elsewhere. La Greca (1980) and Matsuda (1981) propose that the odonate wing has a separate evolutionary origin from other wings, but most authors have instead tried, with limited success, to reconcile the venations.

De Selys, writing in the nineteenth century, created a notation for Odonata without reference to the venation of any other order, but he was not working within an evolutionary framework. His system is formalised by Ris (1909–1919). An early attempt at an inter-ordinal homologisation was Needham’s (1903) application of the Comstock and Needham notation. In this nomenclature the radius and medius of Odonata cross each other in the outer part of the wing. Tillyard (1914, 1917) found against such a crossing in Zygoptera and proposed a system in which veins in the same relative position take a different name in the two main suborders. Lameere (1923), using

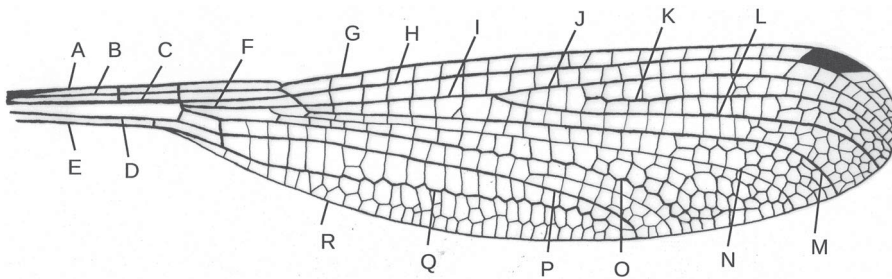


Figure 1. Wing of *Austroargiolestes icteromelas* (Zygoptera), with segments of the main longitudinal veins arbitrarily labelled A-R. Table 1 refers.

wing pleating as a character for determining homology, disputed both Needham's and Tillyard's interpretation of the median vein. Martynov (1924/1930) employed a similar argument but read the "intercalary" veins differently to produce a nomenclature that differs from that of Lameere by one pleat.

Tillyard (1926) proposed that zygopteran venation is plesiomorphic and anisopteran venation derived. This is in contrast to all previous and most later authors, including R&KP, who derive the venation of Zygoptera by reduction from Anisoptera. The now well-established phylogeny (Dumont, Vierstraete, & VanFleteren, 2009; Hasegawa & Kasuya, 2006; Kim et al., 2014; Rehn, 2003; Saux, Simon, & Spicer, 2003) has Anisoptera as a clade within paraphyletic Anisozygoptera, hence supporting Tillyard's conjecture that the ancestral odonate had narrow wings. After minor adjustment (Fraser, 1957; Tillyard & Fraser, 1938–1940) the Tillyard–Fraser notation came to be widely adopted, although variants of Needham's scheme continued in use in North America, and a number of other schemes, including by Hamilton (1972) and Carle (1982), were also adopted by some odonatologists.

Figure 1 shows a typical damselfly (Zygoptera) wing with selected vein segments labelled A-R. In Table 1 each label is linked to its de Selys name and to its short-form label in selected systems.

Structure and origin of wings

The insect wing is a complex structure that develops from an upper wing bud located near the tergum and a lower bud located in a mid-pleural position above the spiracle (Rasnitsyn, 1981). The lower bud is itself a complex organ (Kukalová-Peck, 1978, 1983; Trueman, 1990). Early authors (e.g. Crampton, 1916) had hypothesised an origin of wings from lateral extensions of the tergum. These paranota, originally fixed and perhaps used for gliding, were supposed to have evolved flexible hinges, a musculature and innervation. Rasnitsyn interpreted the upper wing bud as being of tergal origin, hence his terminology of a mixed paranotal-pleural model. Although this terminology is now in widespread use (e.g. Clark-Hachtel, Linz, & Tomoyasu, 2013; Elias-Neto & Belles, 2016; Gullan & Cranston, 2014; Niwa et al., 2010; Prokop et al., 2017; Tomoyasu, Ohde, & Clark-Hachtel, 2017) it is misleading, as will be explained.

The accepted class-level phylogeny (Regier, Shultz, & Kambic, 2005; von Reumont et al., 2011) locates Insecta as a clade within paraphyletic Crustacea, the sister-group being one or more of the crustacean orders Branchiopoda, Cephalocarida and Remipedia. The crustacean leg is hinged from the edge of the tergum, which in most crustaceans is curved such that the first leg podomere is oriented vertically. The crustacean leg has two podomeres more than are found in insects, and there is no pleuron. Kukalová-Peck (1983) proposed that two basal leg segments

Table 1. Selected veins of Odonata under some proposed nomenclatures: refer to Figure 1.

	de Selys	Comstock and Needham	Lameere	Tillyard and Fraser	Hamilton	Carle	Riek and Kukalová- Peck
A	Costal nervure	C	CA	C	wing border	border + CA	PC + C + ScA
B	Subcostal nervure	Sc	CP	Sc	Sc	CP	ScP
C	Median nervure	R + M(+)	R + M(+)	R + MA	R + Cu(+)	R + M(+)	RA + RP(+)
D	Upper sector of triangle	Cu	Scu + P	CuP	P + E	CuP	M + Cu
E	Lower sector of triangle	A'	U, 1A	A'	1A	Cu2	A + J
F	Upper sector of arculus	M	Sr + M	RP + M	Sr + M + Cu	RP + M + CuA	RP + MA
G	Costal nervure	C + Sc	CA	C	wing border	border + CA	PC + C + Sc
H	Radial nervure	R1	R	RA	R	RA	RA
I	Principal sector	M	Sr	RP	Rs + M	RP1	RP
J	Principal sector	M1	Sr1	R2	RsA(–)	RP1	RP1
K	Intercalary sector	M1a	I	IR2	I	I	IR1
L	Nodal sector	M2	Sr2	R3	RsP	RP2	RP2
M	Subnodal sector	Rs(+)	Sr3	IR3	MA	MA	IR2
N	Median sector	M3	Sr4	R4 + 5	MP	MP	RP3 + 4
O	Lower sector of arculus	M4	M	MA	Cu	CuA	MA
P	Submedian nervure	Cu1	Cus, Scu	CuP	P + E	CuP	MP
Q	Lower sector of triangle	Cu2	Pe	1A	A	Cu2	CuA
R	Posterior margin	Posterior margin	Posterior margin	Posterior margin	Posterior margin	Posterior margin	Posterior margin

Vein abbreviations: PC, precosta; C, costa; Sc, subcosta; R, radius; Sr, subradius; Rs, radial sector; M, medius; Cu, cubitus; Scu, subcubitus; Cus, cubital sector; P, plical; E, empusal; Pe, penultimate; A, anal; J, jugal; U, ultimate; I, intercalated. Veins not in their usual orientation are identified by (+) or (–) after the name. Superscripted A' is intended in those nomenclatures that use it to indicate this is not a main vein but is instead a secondary or “back formation” linking a vein to the base of the wing.

(the epicoxa and subcoxa in entomological terminology) became “embedded” in the body wall to create the insect pleuron. However, “embedding” as she envisioned it (Kukalová-Peck, 1983, figures 4–7) raises an insuperable topological difficulty because the ventral surfaces of these podomeres somehow vanish to the inside of the body segment. As well, her model requires the de novo evolution of a sternum (crustaceans have no sternum) and some major re-routing of muscles. If, instead, the two podomeres became short, and broad at their bases, together forming a shallow cone, and if the first podomere became fused to the tergum and to its opposite number along the ventral midline, they would together enclose the body segment exactly as in insects. This model (Trueman, 1990) keeps all cuticular components and musculature intact. The resulting proto-insect would be capable of supporting its own weight in a terrestrial environment. Figure 2 illustrates the evolutionary pathway from an aquatic crustacean ancestor to a terrestrial insect with wing precursor lobes.

The crustacean leg has several side lobes. Those on the first two podomeres are an epipodite on the first podomere, an exite at its distal end, and both an exite and an endite at the distal end of the second podomere (Boxshall & Jaume, 2009). Shortening and broadening the two podomeres brings all four of these lobes into positions from which they might together form a wing. On this

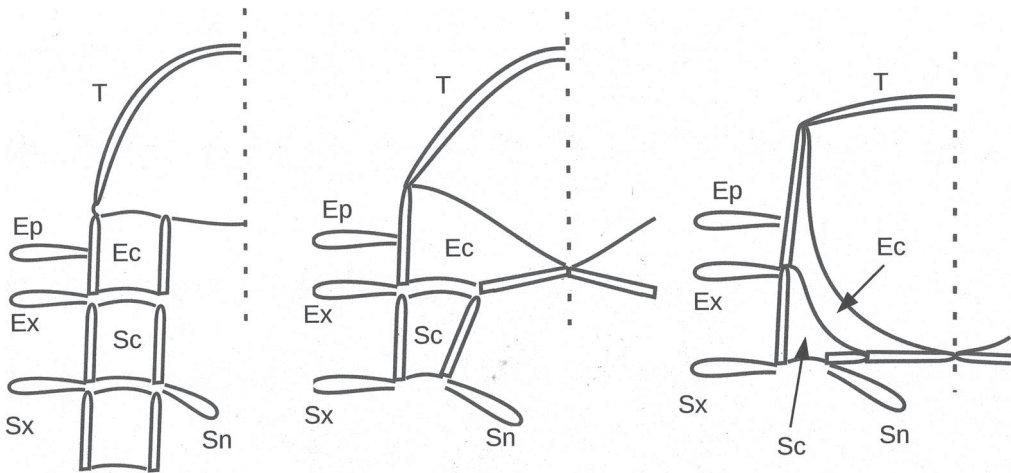


Figure 2. Two leg segments, end on end, become broadened at their base until they enclose the entire side and underside of the body segment. Half-sections through a thoracic segment, diagrammatic. Left: the condition in Crustacea. Centre: an intermediate condition. Right: the insect thorax. T, tergum; Ec, epicoxa; Sc, subcoxa; Ep, epipodite; Ex, epicoxal exite; Sx, subcoxal exite; Sn, subcoxal endite.

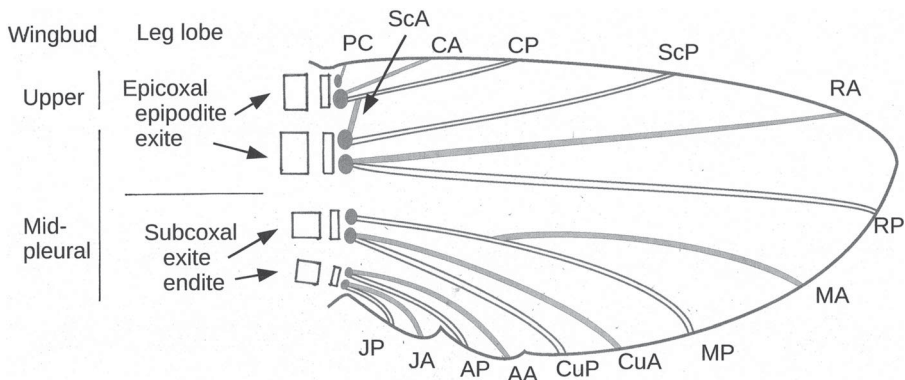


Figure 3. The arrangement of leg lobe derivatives and wing veins in the wing of a hypothetical pterygote ancestor. Diagrammatic. Upper surface (+) veins are shaded, lower (-) veins unshaded.

model the upper wing bud is formed from the epipodite while the pleural bud is a fusion of the epicoxal exite, the subcoxal exite and the subcoxal endite.

In the Crustacea each lobe is a flattened sac that articulates on a simple hinge. Movement is achieved by muscles that pull on the upper and lower sclerites in the hinge joint. There are no veins, but the cuticle is strong enough throughout to take the stresses imposed by the muscles. The insect wing articulation comprises a row of four such hinges, with two longitudinal vein pairs extending from each hinge. Figure 3 shows the arrangement. The inter-vein cuticle undergoes a truncated development and the haemolytic and cellular contents are lost (see next section), producing a membrane light enough for flight but needing mechanical support, including at the hinge joint attachment points.

The epipodal hinge subtends the precostal (if present) and the costal veins. The three hinges of the pleural wing bud support, in order, the subcostal and radial veins, the medial and cubital veins, and the anal and (if present) the jugal veins. In Neoptera and diaphanopteroid Palaeoptera the sclerites to which the muscles attach are not fused or show only limited fusion (there is minor

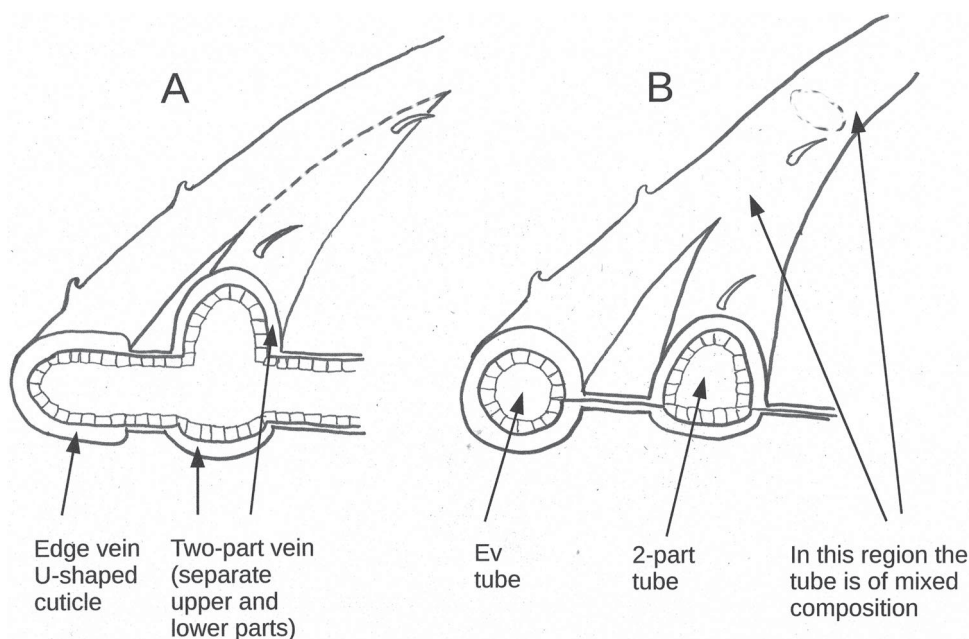


Figure 4. A two-part longitudinal vein approaches the edge vein at a shallow angle. (A) Prior to eclosion the two halves of the longitudinal vein are separately contiguous with their respective arm of the edge vein. (B) In the definitive wing blade part of the wing margin tube is a composite of both veins.

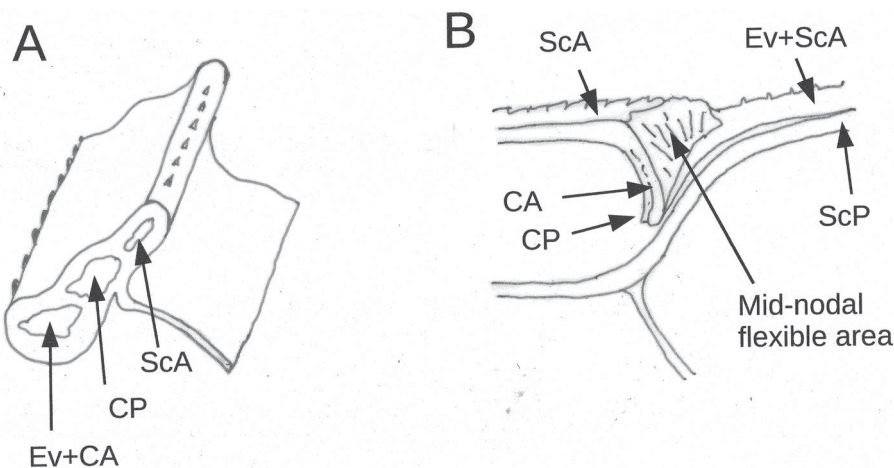


Figure 5. At the front of the wing. (A) A transverse section through the Anterior Spar showing the three components (Ev + CA), CP, and ScA. (B) The nodus from below, the wing base is to the left. At this distal end of AS the veins CA and CP lie bodily below ScA. The mid-nodal flexible area is formed by a sinus of ScA.

variation by order), and the wing can be folded back along the body. In remaining Palaeoptera including the two extant orders the hinges of the pleural bud have become fused, and the anterior branch of the subcosta is inflexibly joined to the posterior branch of the costa, such that the wing can no longer be folded. Figure 1.7 of CSIRO (1991) juxtaposes the three extant alternatives in a very clear fashion. Martynov (1924), following the then-prevalent paranotal model of wing origin, named Palaeoptera for their supposedly primitive wing articulation, but non-folding is the derived condition.

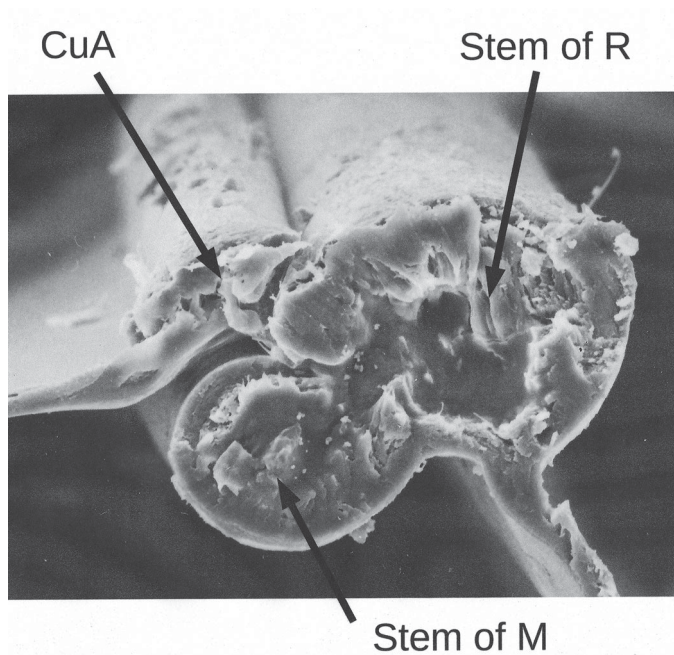


Figure 6. The triple stem in *Diphlebia lestoides* (Zygoptera). The wing anterior margin is to the right.

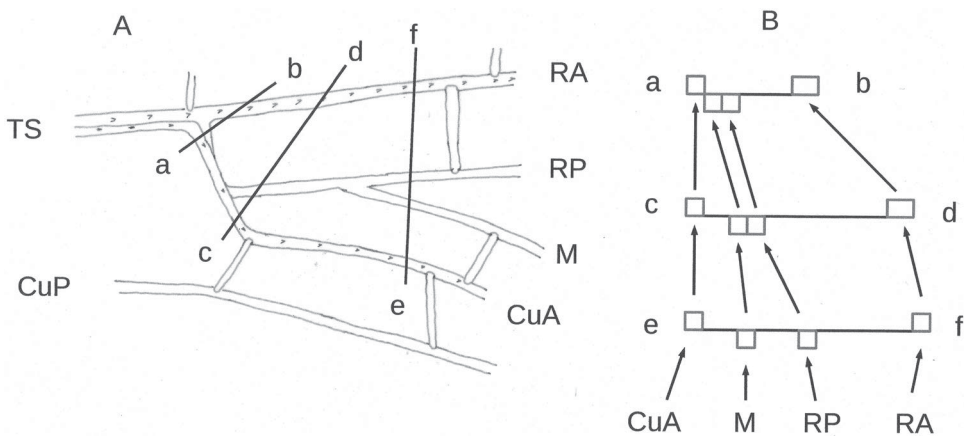


Figure 7. At the arculus, the first component of TS divides to give RA and RP. Stem M turns back behind RP and CuA turns back behind M. After a short distance, RP + M turns towards the wing tip. CuA may turn with RP + M or, as here, continue for a short distance before turning. Further along the wing, M and RP separate. (A) A sketch showing the vein relationships (semi-diagrammatic, compressed laterally as compared to any known species). (B) Transverse sections through a–b, c–d and e–f, showing (diagrammatically) the positions of the ridges, on which cuticle is laid down, in relation to the midline between the two wing surfaces.

The upper wing bud lies on the distal side of the hinge line between the tergum and pleuron, where the epipodite was formerly located. A tergal origin of this wing bud would necessitate the loss of that lobe and its musculature, and the de novo evolution of its paranotal replacement. A more parsimonious interpretation is that the upper wing bud is that original lobe and the entire

wing has evolved from leg components. No part is of tergal origin and there was never a non-motile, that is, a paranotal wing precursor.

Recent gene expression data lend support to these hypotheses. Wing-related genes including *nubbin*, *vestigial* and *apterous* are expressed separately in each wing bud, indicative of serial repetition by leg podomere, while *wingless* is expressed along the sternal midline as well as on the tergal margin, consistent with tergo-sternal continuity of the epicoxa (Averof & Cohen, 1997; Niwa et al., 2010). Experiments involving *disheveled* have shown that disruption to *wingless* results in an abnormal sternum as well as abnormalities along the tergal margin (Clark-Hachtel et al., 2013). Bruce and Patel (2018) have used CRISPR-Cas9 knockouts of leg gap genes to confirm that the entire wing evolved from what in Crustacea are leg segments.

Wing veins – structure and disposition

A vein is a linear region of thick cuticle on the surface of the wing. Cuticle is a layered, non-cellular product secreted by the dermal cells. The process of wing cuticle formation has been studied in *Drosophila* (Fristrom, Wilcox, & Fristrom, 1993; Kimura, Kodama, Hayasaka, & Ohta, 2004) but so far as we are aware not in Odonata. The wing of *Drosophila*, at the stage when adult epicuticle is being secreted, is a sac-like structure filled with haemolytic fluid. This fluid is withdrawn until the putative upper and lower surfaces come into contact throughout the areas that will become transparent membrane, and inter-epithelial connections are formed in those parts. The wing fills with fluid for a second time while the meso and endocuticles are being secreted, and then, after eclosion, the haemolytic content is withdrawn as the wing dries. The epithelia in the membranous areas break down and are resorbed, leaving apposed cuticles that bond back-to-back, while in the parts that did not make contact at the first apposition the epithelia persist to form haemolymph-filled tubes which are the veins. Fristrom et al. (1993, figure 1) provide a clear summary while Pass, Tögel, Krenn, and Paululat (2015) give additional detail. In Odonata, Appel, Heepe, Lin, & Gorb (2015) have shown that the cuticle along the veins is not just thicker but is composed of more layers than that in the membranous areas. This is consistent with some such two-stage process occurring also in Odonata.

The dermal ridges along which the longitudinal veins of Odonata form are present during late-larva instars (Tillyard, 1917). A nerve cord, serving the multicellular organs including sensory setae that typically run on the ridge side of each vein, runs along the midridge. Most veins also enclose a branch of the tracheal system. In contrast with the longitudinal veins, crossveins develop only at the final ecdysis, develop more or less equally on both wing surfaces, rarely enclose a nerve or tracheal tube, and after alignment may be almost solid.

The origin of wings from four lobes on two podomeres indicates that ontogenetic development should be compartmentalised. Garcia-Bellido, Ripoll, and Morata (1973) observed these compartments in *Drosophila*. The highest-level or first-formed boundary is situated, as would be expected, along the podomere boundary that runs behind the radius and in front of the medius (Garcia-Bellido et al., 1973, figure 1d). The physical structure of veins, together with this developmental compartmentalisation, places limits on how the pattern of the venation can evolve. Two veins on the same surface cannot cross each other because a dermal cell cannot secrete two competing cuticles. A longitudinal vein cannot lose its base yet retain its distal part because the distal part would lose its connection to the circulatory system, although desclerotisation at the base is permitted if the ridge/tube structure persists. The distal part of a vein cannot become secondarily attached to a different vein pair because development, including of the enclosed nerve cord, is compartmentalised in line with the original leg and lobe segmentation. A tubular vein cannot change its orientation from one wing surface to the other, or not while retaining its original nerve

cord and any associated surface-specific organs, while surface-specific organs of opposite orientation must arise de-novo. Permitted changes include that the membranous field between two veins may become so narrow as to result in a double vein, or so thickened that veins and the intervening transparent field become one solid mass. A vein can thicken or may atrophy. Two veins in parallel and in contact might form a single tubular structure, and over evolutionary time two veins might merge if both are on the same surface and on the same original lobe, but merger would not be expected if they are on opposite surfaces or are separated by a developmental boundary.

Textbooks that are arranged by taxon typically provide illustrations of the venation of each order, and there are myriad other illustrations in species descriptions and generic revisions. From this literature some generalities emerge about the usual degree of development of each vein, its position relative to other veins, its relation to the articular sclerites, and the orientation of its major ridge. These factors all aid in working out which vein is which, and have been employed extensively in arguments for and against alternative nomenclatures. One further factor, neglected in past nomenclatures for Odonata, is whether the vein divides at its base or whether it is stemmed.

The eight-vein hypothetical “groundplan” venation of Kukalová-Peck (1983, figures 13–15) has all eight vein pairs separating at the base, but in two respects actual insects do not conform. The radial vein is stemmed in some Plecoptera and in the non-odonatoid palaeopterans Calvertiellidae, Diaphanopterodea, Megasecoptera, *Permothis* and *Protoreisma*, while the median vein is stemmed in all orders, as in our Figure 3. Hence a stemmed radius may occur in the odonatoid orders including Odonata and a stemmed medius is to be expected.

Many nomenclatures omit the sclerotised margin of the wing or consider it not to be a vein, but it fits our definition. It is not one of the eight pairs of two-part longitudinal veins but it is universally present and histologically of the same composition as other veins. It functions to stiffen the edge of the wing, to dissipate edge stresses and to guard against tearing. Being unmusculated at both its anterior and posterior articulation with the body wall it is a passive player in wing movement. The primary cuticular product, by necessity due to its location along the edge, is a ribbon of cuticle that is broadly U-shaped in transverse section. As the wing dries the arms of the U collapse inward to form the tube. Along the anterior margin where two-part veins approach this Edge vein, Ev, at shallow angles, each half of the two-part vein meets the corresponding open end of the U and merges into it as illustrated in Figure 4. The margin tube is a composite of Ev with, in turn, PC, CA, CP, ScA, ScP and RA. In the posterior half of the wing the two-part veins tend to approach at a steep angle and the greater part of the wing margin is formed from Ev alone.

Applying this model to Odonata

At the front of the wing, between the base and the nodus, the anterior vein system comprises a strongly sclerotised Anterior Spar we designate as AS. Transverse sections reveal three membrane-lined tubes enclosed in heavily sclerotised cuticle; see Figure 5a. The lowermost tube is Ev with CA. The middle tube is CP and the hindmost, uppermost tube is ScA. Vein ScA can be seen to originate on the axillary plate, high above the plane of the wing, from where it turns forward while descending steeply to form the upper edge of the spar. Spar AS thus incorporates two entire membranous fields of the wing, the CA/CP and CP/ScA fields. Two rows of short, stout setae run the length of the spar. The lower row is on Ev, the upper is on ScA. Where R&KP identify this section of wing border as $Pc + C + ScA$ its true nature is $(Ev + CA) + (CP) + (ScA)$, the parentheses indicating the tubes. An antenodal crossvein,

Ax0, ignored in some vein nomenclatures, runs at the base of the transparent membrane. The precosta can be made out only as a faint thickening on the upper humeral plate proximal of Ax0.

Both CA and CP terminate on the proximal side of the nodus. Their curled ends can be readily seen in cleared specimens. Veins Ev and ScA and the two rows of stout setae continue. On the lower wing surface, ScP turns forward, then outward, to merge gradually into the wing margin proximal of the pterostigma. The wing margin across the nodus is Ev + ScA. Figure 5b shows a ventral view. The flexible area within the nodus is not a conventional membranous area but appears, from its relationship to adjacent veins, to be an inflated and desclerotised section of ScA. The postnodal margin is not, as R&KP have it, PC + C + Sc. For a short distance it is (Ev + ScA) + ScP but towards the pterostigma it is Ev + ScA and closer to the tip it is Ev + ScA + RA as a single tube.

Proximally the first membranous field begins along the rear edge of ScA from where it descends steeply to ScP. The next field ascends equally steeply. In this part of the odonate wing the vertical measurement from ScA to ScP may exceed the horizontal measurement from Ev to the vein complex behind ScP.

That complex appears to consist of two veins in parallel on the upper surface. It is a structure unique to and characteristic of the odonatoid orders. Nomenclatures differ greatly. R&KP see RA with RP+, the latter having been translocated to the upper surface. Tillyard and Fraser (1938–1940) see R with MA, the latter having lost its stem and its posterior branch. Needham (1903), Lameere (1923), and Carle (1982) see R with M+, again invoking a change in surface. Hamilton (1972) sees R with a stemmed Cu. If R&KP were correct it is hard to see why two branches of the same vein, in lengthwise contact for more than 300 million years, have not merged or fused. We must take a closer look at this apparent double vein.

Viewed from above, two upper surface veins run side by side. The join between them is somewhat ragged and varies in detail from specimen to specimen as if two ribbons of liquid cuticle made contact as they dried. Viewed from below there are again two visible veins but the line of contact is smooth and faint as if seen through a layer of cuticle. A transverse section (Figure 6) shows there are, in fact, three veins. The first and third are visible from above. From below the second vein hides the third and only the first and second are visible. From their relative positions these are veins R, M, and CuA, each in its usual orientation, with R stemmed as in many Palaeoptera, and with M stemmed and Cu unstemmed as in all insects.

A simple experiment will confirm the three-vein structure. If a short piece of wing from a dried specimen is immersed in a weakly caustic aqueous solution (we use 2–3 crystals of commercial drain cleaner in a watch-glass of tap water), bubbles form inside each tube as the soft tissues dissolve. The reaction may take hours or days according to the strength of the solution, and is best done slowly so the two halves of each vein do not come apart. There are always three separate lines of bubbles in this section of the wing; one in each upper tube and one in a tube below and between those tubes.

At the distal end of this Triple Stem, which we designate TS, stem R throws a lower surface branch RP as in other orders. The median stem turns back behind RP while CuA follows closely. Figure 7 shows the spatial relationship and how RP, M and CuA later separate. More distally, RP divides twice, as in other orders, to give an upper-surface branch between two lower-surface branches. The upper-surface branch is vein IR1 of the R&KP system. Stem M likewise divides in its usual way, throwing an anterior upper surface branch, MA. This is vein IR2 of R&KP. The continuation of M on the lower surface is the usual MP. The medial field, MA/MP, is much expanded in Anisoptera, and a mid-field longitudinal vein with no basal connection runs from the wing margin towards the MA-MP branch point in some families. This base-free, nerve-cord free vein is evidently developed from the mid-line of the rows of polygonal cells which fill the

distal part of this field in related families. The name Median Supplementary vein, MS, seems appropriate.

Vein CuA, on the upper surface, having turned back to follow the line of RP + M on the lower surface, turns outwards to run unbranched to the wing border as in other orders. The CuA/CuP membranous field is much expanded in Anisoptera and a supplementary vein of similar construction to MS is present in some families. The best available name, without causing great confusion with past nomenclatures, would be the Cubital Supplementary vein, CuS. Both MS and CuS are chiefly developed on the lower surface. Whether they evolved once or on more than one occasion will become clear when the family-level phylogeny of Anisoptera has been better established.

In R&KP nomenclature the base of the longitudinal vein behind TS is M + Cu. However, neither the “bubble” technique nor scanning electron microscopy finds any evidence of a second tube in this vein. Also, according to R&KP, a proximal section of M has disappeared completely such that MA + beyond the arculus has become secondarily attached to RP + . Such an event involves re-routing the median vein’s nerve cord from the lower to the upper surface, and also from behind to in front of the mid-wing developmental boundary, then back again. As stated in our Introduction these changes are not plausible. Given that the posterior component of the triple stem is CuA, the lower-surface vein immediately behind it is undoubtedly CuP. This vein can be seen to begin near the anterior proximal corner of the CuA/CuP field, from where it runs briefly back before turning distally. The basal part of this field is lightly sclerotised as if for additional strength and the part proximal of CuP, which in a neopterous insect would consist of flexible cuticle along a flexion line, is sclerotised. Ninomiya and Yoshizawa (2009), who have homologised all the hinge joint sclerites of Odonata with those of other orders, expressed surprise that this region is devoid of sutures and muscle insertions. The explanation is that while all the usual sclerites and muscles are present they are crowded together at the anterior edge of the field.

The CuA/CuP field in Zygoptera incorporates the discoidal cell or quadrilateral. This cell is widened distally in Anisoptera and has become braced across its mid-line to form the hypertriangle and triangle. The brace is open to CuP at its proximal end but is pinched almost shut, like a crossvein, at its distal end. It is best interpreted as a forward branch of CuP rather than as a common crossvein.

In Meganeuridae, *Ditaxineura*, *Kennedya*, *Permolestes* and *Epilestes*, but not in other fossil Odonatoidea, a weak, quasi-longitudinal, upper-surface vein runs within the basal cell of the CuA/CuP field. This vein begins near the anterior proximal corner of the cell and finishes abruptly on CuP. Various nomenclatures consider it a remnant of one or another main vein or as a crossvein. In R&KP nomenclature it is the stem of M after translocation to the upper surface. We observe that in Odonata a thin, largely upper surface, crossvein runs through the sclerotised area proximal of the transparent membrane within this field. Given the similarity in start and end points and in general direction, the quasi-longitudinal vein of the fossil odonatoids is, in all probability, this same crossvein. Anomalously, the vein is described from a single anisozygopteran fossil, *Tarsophlebiopsis mayi*. One of us (JT) examined the holotype and found this supposed instance to be an artefact of preservation. A fold runs through this wing fragment from its broken-off base to a point beyond the open discoidal cell, giving the impression of an extra vein.

Behind CuP, the final longitudinal vein of the odonate wing is on the upper surface. From its structure and position this is the anterior vein of the anal pair, vein AA of other insects. Veins AP, JA and JP are wholly absent. However, along the rear edge of the zygopteran wing Ev runs for some distance alongside AA and is variably welded to it in the same ragged manner as CuA is welded to R. This indicates that some narrow remnant of the AA/AP field persists. In Anisoptera this weld region is restricted to a short section proximal of the anal triangle or, in species or

the sex with no anal triangle, at the extreme basal corner of the wing. Given the phylogenetic relationships of the suborders the zygoteran condition is plesiomorphic, and thus, contra R&KP and several other nomenclatures, in Anisoptera the remnant AA/AP field has become secondarily expanded. In Anisoptera vein AA may branch from one to several times, always on the upper surface, to form a neo-anal field.

The membrane between these branches is supported by fields of polygonal cells. R&KP and some other nomenclatures label these an archedictyon, which was the term for a venation supposed to have been present in the fixed, paranotal proto-wing before hinges, longitudinal veins and musculature evolved. However, the observed venation cannot predate clade Anisoptera, and given the constitution and origin of the insect wing there can be no archedictyon in any insect order.

Much has been made, in most odonate nomenclatures, of a strong crossvein termed the anal crossing, Ac, located between CuP and AA near the distal end of the petiolate section in Zygoptera, and, while at times weakened, in the corresponding position in Anisoptera. Interpretations include that AA here separates from CuP (implying the basal section of the final longitudinal stem is not a main vein but a back-formation), or that vein Cu (inexplicably with a stem), or else CuP here turns back from a combined M with Cu stem. We observe Ac to be equally developed on both wing surfaces and almost completely solid. The junctions at either end are unusually thick and the haemolymph channel is pinched almost shut. Donoughe, Crall, Merz, and Combes (2011) found there to be no buffer of the shock-absorbing protein resilin at either end of this vein, which is unusual for a crossvein. We consider Ac to be a crossvein, its function in Zygoptera being to tie CuP firmly to AA. This functional constraint is partially relaxed in Anisoptera in which the neo-anal field is developed.

Interpretation

The odonate wing has all the veins of a generalised insect except that AP and J are suppressed. The evolutionary history looks to be extremely simple. Stem Palaeoptera experienced narrowing and fusion of the hinges on which the wing articulates. Complete closure of the proximal R/M and M/Cu membranous fields occurred in stem Odonatoidea (Carboniferous), producing the triple stem. In Odonata (Permian), further narrowing along the proximal anterior margin of the wing and a reduction in the length of the costa created the anterior spar. By the addition of a strong tie, Ac, between CuP on the underside and AA on the top side at the rear of the wing, the wing action is converted to one in which two inflexible levers, AS and TS, power a distal, paddle-shaped blade. This is the wing action of Zygoptera. Some time later, one lineage evolved a more robust body form, possibly in conjunction with an episode of near-terrestrialism since the caudal gills also were lost at this time and rectal gills acquired. Rectal gills released the larva from having to source almost all its oxygen from the external body surface. The more heavily-set body called for greater lifting power than the petiolate action could provide. Induced expansion of the medial and cubital fields and the de-novo evolution of a neo-anal field in Anisozygoptera led to the fully developed anisopteran, non-petiolate venation. These changes date, in all probability, to the Triassic, since almost all extant anisopteran families are known from the Jurassic.

We are now in a position to add a column to Table 1. In our system, vein segments A-E are, respectively, Ev + CA + CP + ScA, ScP, R + M + CuA, CuP and AA + Ev. Vein segments F-L are, respectively, RP + M, Ev + ScA + ScP, RA, RP, RP1, IR1 and RP2. Vein segments M-R are, respectively, MA, MP, CuA, CuP, AA and Ev.

Table 2. Principal veins and vein complexes of Odonata

Ev	Edge vein	The sclerotised edge of the wing
AS	Anterior spar	Anterior proximal corner to nodus N; a vein complex comprising Ev + CA, CP, and ScA, the former CA/CP and CP/ScA fields between them heavily sclerotised
PC	Precosta	Visible only as a linear thickening along the margin proximal of Ax0
C	Costa	Unstemmed, as CA + and CP–; from the humeral plate to N
Sc	Subcosta	Unstemmed, as ScA + and ScP–; from the axillary plate
ScA	Subcosta anterior	The third (rear, uppermost) component of AS and the main component of the anterior margin distal of the nodus
ScP	Subcosta posterior	First free vein behind AS; turns forward to form the distal side of the nodus then merges into the anterior margin
Ax0, 1, 2	Antenodal crossveins	Strong crossveins linking AS to R above the line of ScP
N	Nodus	Short section of the anterior margin where C terminates, ScA is expanded to form a flexible hinge and ScP joins the wing margin
TS	Triple stem	The odonatoid mid-basal vein complex from the wing base to the arculus; components are stem R +, stem M–, and CuA +; intervening membranous fields R/M and M/Cu are suppressed; R and CuA cuticles make secondary contact as the wing dries
R	Radius	First component of TS; branches at the arculus to give RA + and RP–
Arc	Arculus	Short sections of RP, M and CuA at the distal end of TS, together with any supporting crossveins
RP1, RP2	Branches of RP	Distal lower-surface branches of RP–
IR1	“Intercalated” vein	Distal upper-surface vein between RP1 and RP2
M	Medius	Stem M– runs under R + and CuA + along TS; at the arculus it turns back along with RP–; in the outer wing it throws an anterior upper-surface branch MA +; the continuation on the lower surface, MP–, runs unbranched to the wing border
MS	Medial supplementary	A lower-surface longitudinal vein without basal connection, located within the MA /MP field in some lepidopteran and anisopteran families; interpreted as a secondary straightening of the mid-line of the field of polygonal cells that fills the outer part of this field in related families; the phylogenetic distribution is such that MS may have multiple origins
Cu	Cubitus	Unstemmed as CuA + and CuP–, enclosing the cubital field (which includes the discoidal cell of Zygoptera and the hypertriangle and triangle of Anisoptera)
CuS	Cubital supplementary	A lower surface vein in the distal part of the cubital field; formed in the same manner as MS and with a similar but not identical phylogenetic distribution
AA	Anal vein	The vein AA + of other orders; the anterior branch of the anal vein pair
Ac	Anal crossing	Not a crossing but a crossvein connecting CuP firmly to AA

A proposed nomenclature

Our proposed nomenclature is set out more fully in Table 2 and illustrated in Figures 8, 9. PC extends no further than crossvein Ax0 and so is not visible in these diagrams. The anterior spar, AS, is a three-way fusion of Ev + CA with CP and ScA, the intervening fields being strongly sclerotised. Ev forms the lower, front edge of this structure, ScA is the upper edge. Both branches of C terminate on the proximal side of the nodus. Both Ev and ScA continue through N, after which they are joined by ScP which then merges slowly on the underside of the wing. RA merges into the wing border before the wing tip. Branches of RP, M, Cu, and finally AA meet the posterior border of the wing. The final trace of ScA, as marked by its row of blunt setae, ends some way short of where the most posterior branch of RP meets the wing border. To a first approximation the anterior margin of the wing, from base to nodus, is (Ev + CA) + (CP) + (ScA), while the margin from N to the pterostigma, Pt, is Ev + ScA + ScP, and beyond Pt it is Ev + ScA + RA. The posterior margin is Ev alone, except at the base where Ev is bonded lengthwise against AA.

The triple stem is (R) + (M) + (CuA). RP separates from RA at the arculus and M turns back with it on the underside, CuA following the line of the developmental compartment on the upper

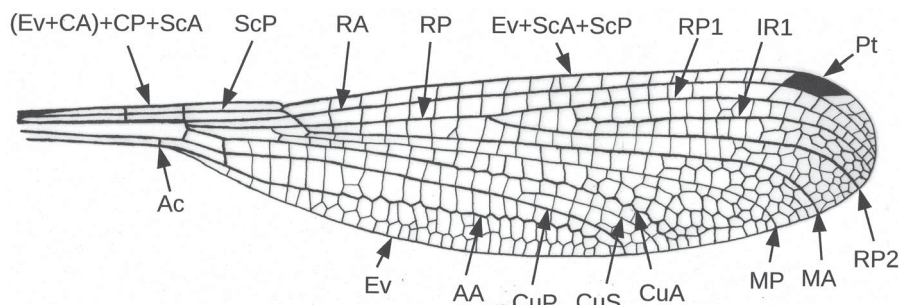


Figure 8. Wing of *Austroargiolestes icteromelas* (Zygoptera) labelled in accordance with the proposed system.

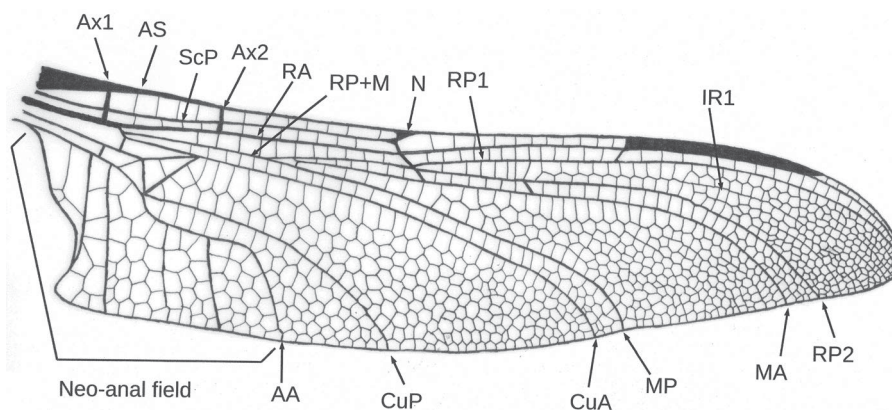


Figure 9. Hind wing of male *Petalura gigantea* (Anisoptera) labelled in accordance with the proposed system.

surface. Veins RP + M together turn towards the wing tip and then separate. RP branches once to give RP1 and RP2. The upper-surface branch between them, IR1 of R&KP, has been interpreted as an intercalary vein rather than a true branch of the lower-surface RP vein. We propose to keep that nomenclature because it is known to odonatologists and because nomenclatures in use for other orders are not consistent. However, we do not mean to imply that the evolutionary origin of this upper-surface vein is by secondary growth inwards from the wing margin.

Beyond where stem M separates from RP it extends an anterior, upper surface branch, MA. In lestoid Zygoptera and some Anisoptera a longitudinal vein without basal connection runs inside the medial field. We concur with others that this is a supplementary vein. To avoid confusion with existing nomenclatures we name it the median supplementary, MS. In evolutionary terms, it has developed inwards by cell margin alignment, starting at the wing margin.

The CuA/CuP field encloses the discoidal cell, which secondarily is much expanded in Anisoptera. The anterior side of the triangle is a forward branch from CuP. In the lestoid families and Anisoptera a supplementary vein without basal connection may run inside this field. To avoid confusion with existing nomenclatures we name it the cubital supplementary, CuS. A further distinction between the intercalary IR1 and the two supplementaries MS and CuS is that the former is developed on the upper wing surface while the two latter are lower surface veins.

Behind CuP, the final longitudinal vein in Odonata is vein AA of other orders. In Anisoptera this vein is pectinately branched to produce a neo-anal field, the venation of which has no homologue elsewhere.

Summary and conclusion

Our proposed system completely reconciles the venation of Odonata with that of other winged insects. No veins other than AP and J are missing. No veins mysteriously relocate from one wing surface to the other. No vein loses its base, becomes secondarily attached to a vein of another series or of another original leg lobe or podomere, or undergoes change that invokes any other evolutionary impossibility. Our system contains no bridge veins or back-formations, and the homologies to other orders are fully resolved.

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